Amer. Malac. Bull. **25**: 87-95 (2008)

The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora)*

Stephaney S. Puchalski[1], Douglas J. Eernisse[2], Claudia C. Johnson[1]

[1] Department of Geological Sciences, Indiana University, 1001 E. 10th St., Bloomington, Indiana 47405, U.S.A., spuchals@indiana.edu

[2] Department of Biological Science, California State University Fullerton, Fullerton, California 92834-6850, U.S.A.

Abstract: The chiton fossil record is richer than previously reported in the literature. A newly compiled database comprised of Cambrian to Pleistocene fossil chitons totals 2594 occurrences of 900 species. Of the 900, 430 are named species known only as fossils, 123 are extant species that also have a fossil record, and 247 are indeterminate taxa. Most of the database (61%) consists of fossil chiton occurrences reported from localities other than type localities. A preliminary analysis of the data using the collector curve method suggests that the chiton fossil record has not been adequately sampled by geographic regions or geologic time. The fossil record of chitons is incomplete, sporadic, and geographically limited because the sampling record has been incomplete, sporadic, and geographically limited. The current database comprises enough information to discern diversity patterns throughout geologic time, but whether the patterns are real or artifacts of sampling inadequacy remains to be investigated.

Key words: collector curve, database, sampling record, fossil record completeness, sampling adequacy

Data analysis is a fairly recent approach to investigating and discerning patterns in the fossil record (Raup 1976a, 1976b, Benton 1993, Smith 2001, Alroy *et al.* 2001, Westrop and Adrain 2001, Sepkoski 2002, Tarver *et al.* 2007, and others). Incompleteness in the data, however, including incompleteness of the fossil record itself, introduces error in interpretation of observed patterns. Both taphonomic and sampling biases cause incompleteness and affect the amount of data available for analysis (Benton 1998, Benton *et al.* 2000, Tarver *et al.* 2007), but taphonomic biases are better understood than sampling biases. Few researchers have addressed the latter issue (Tarver *et al.* 2007 and references therein). Assessment of sampling bias is essential to evaluating the adequacy of the fossil record. Understanding the causes of incompleteness allows paleontologists to use statistical methods to correct for errors in order to differentiate real patterns from apparent trends.

Despite a Cambrian to Holocene fossil record, chitons (Polyplacophora) may be less well sampled than other shell-bearing fossil fauna such as brachiopods, gastropods, bivalves, and cephalopods that have similarly long but 'good' fossil records. Although significant numbers of chiton valves (400 or more) have been recorded from some localities (Itoigawa *et al.* 1976, Bischoff 1981, Baluk 1984, Laghi 1984, Bellomo and Sabelli 1995, Cleveringa *et al.* 2000, Hoare and Pojeta 2006, Sigwart *et al.* 2007), most extinct chiton species are represented by relatively few valves that are rare compared to other taxa in an assemblage. Even when characterized as 'exceptionally abundant,' the valves are still uncommon in comparison to other taxa. For example, chiton valves were only 7% as common as bivalves found at the same Silurian localities in Gotland (Cherns 1999). Inadequate sampling thus may have affected patterns of chiton diversity and distribution reported in the literature (*e.g.*, Sepkoski 2002, Cherns 2004, Puchalski 2005). Chitons reportedly are most diverse in the Holocene (Smith 1960, Lindberg 1985, Benton 1993). About 900 modern chiton species inhabit mostly shallow coastal waters and are ubiquitous on modern rocky shores in all oceans and at all latitudes worldwide (Kaas and Van Belle 1985). In comparison, the reported chiton fossil record ranges between 256 and 368 fossil species (Smith 1960, Van Belle 1981, Eernisse 2001, Schwabe 2005), sporadically distributed through geologic time and geographically limited mostly to the North American, European, and Australia-New Zealand regions (Van Belle 1981).

This study assesses sampling bias in the chiton fossil record using the collector curve approach with a database on fossil chiton occurrences. The occurrence data also were used to show patterns in chiton diversity from the Cambrian to Pleistocene.

MATERIALS AND METHODS

Database compilation

The initial database containing 336 fossil chiton species was compiled by Eernisse (2001). The database included

---

* From the symposium "Advances in Chiton Research" presented at the joint meeting of the American Malacological Society and Western Society of Malacologists, held 29 July to 3 August 2006 in Seattle, Washington.

suborders, families, genera, type locality information, geologic period, year of publication, and museum information (*e.g.*, type kinds and numbers). The database was expanded by the first author (S.P.) to include additional occurrences of fossil chitons from the Cambrian through the Pleistocene at type and other localities. An occurrence was defined as a reported difference in geographic location of collection (latitude and longitude) or taxonomy (species). No distinction was made between geographic and taxonomic occurrences. Taxonomic differences were determined by cross-referencing the literature to account for synonymies and updating original taxonomic assignments when systematic relationships were reevaluated in later references. Taxonomic occurrences with indeterminate relationships were grouped in the genus "Indet." whether originally reported as indeterminate, unidentified, "polyplacophoran," or "chiton" regardless of whether or not the fossils were figured and/or described. The database was developed further to include modern latitude and longitude coordinates of the collecting locality, reported numbers and types of valves, authors' reasons for publication, geologic stage, and other geologic information such as lithology and general fossil associations whenever possible. The primary data sources were published reports including descriptions of fossil species, but occurrences obtained from unpublished sources (*e.g.*, online museum collection databases) also were included.

All taxa regarded as invalid chiton fossils were excluded from this preliminary analysis of the data. For example, some Early Cambrian "polyplacophoran" fossils from China (Yü 1987) may be only superficially similar to chitons (Qian and Bengtson 1989) or may be valid chiton taxa (Yü 2001, Schwabe 2005). The fossils have an overlapping series of plates that are much smaller than other chiton valves but similarly differentiated into three types with distinct areas on the dorsal surface and shell layers consisting of 'articulamentum' and 'tegmentum.' Qian and Bengtson (1989) argue that the poorly preserved 'plates' show very few structural details and are not articulated with one another but rather represent a series of successively larger growth increments deposited on the inner side of sclerites. After restudying the specimens, Yü (2001) maintains that the fossils are indeed polyplacophorans closely related to *Gotlandochiton* Bergenhayn, 1955, *Priscochiton* Dall, 1882, *Chelodes* Davidson and King, 1884, and questionably *Glyptochiton* de Koninck, 1883. However, the first three genera are paleoloricates that are distinguished from more modern chitons in lacking articulamentum, a character that does not appear in undoubted chiton fossils until the Carboniferous (Sirenko 2006). The implication that chitons with articulamentum "gave rise" to chitons without articulamentum that then evolved into chitons with articulamentum is problematic. The remaining characters described by Yü (1987, 2001) are not necessarily exclusive to chitons. The Lower Cambrian taxa thus were rejected as valid chiton species for the purposes of this study.

The completeness of the sampling record was assessed using all fossil chiton occurrences including named species, which represent less than 17% of the entire dataset. Debates on the validity of some taxa and frequent changes in chiton systematics made it difficult to directly compare the number of named species to previous catalogues of fossil chitons (*e.g.*, Smith 1973, Van Belle 1981, Smith and Hoare 1987, Schwabe 2005). These catalogues were used in most cases to determine the validity of taxa for this study, but some catalogues are incomplete and the authors did not always agree on validity. Some species considered valid for the purposes of this study thus may not have been considered valid in previous catalogues. In cases of more recent publications, omissions from previous catalogs, or where published views conflicted regarding synonymies or validity of a particular fossil as a chiton, validity was determined by S. Puchalski using the primary literature. For example, an exhaustive literature search revealed multiple species not included in Van Belle's (1981) monograph (*e.g., Pterochiton tripartitus* Ebert, 1889 and *Pterochiton silesiacus* Ebert, 1889) that were considered to be valid chiton species. Additionally, *Chitonellus hancockianus* Kirkby, 1859, *Chitonellus antiquus* (Howse, 1848), and *Chitonellus distortus* Kirkby, 1859 named and described by Kirkby (1859) in Permian limestone at Tunstall Hill, England were listed as "no chiton" by Van Belle (1981) and rejected as polyplacophorans by Smith and Hoare (1987). The reported occurrence of these taxa was accepted as valid for this study under the name *Diadeloplax antiqua* (Howse 1848) based on Hoare and Mapes (2000), who recognized the three taxa as a single multiplacophoran species. The multiplacophorans were accepted as valid chiton taxa because Vendrasco *et al.* (2004) referred the multiplacophorans to Class Polyplacophora. The list of valid taxa and associated geographic and temporal data used in this preliminary analysis is available at: http://www.biology.fullerton.edu/deernisse/fossilchitons/. The complete database will be made available after further analysis.

The data were divided into several different groups for convenient analysis. Countries of occurrences were grouped into geographic regions (Table 1) that approximate modern continents (Tarver *et al.* 2007). Valid chiton taxa were separated into seven taxonomic groups consisting of: (1) named extinct species known only as fossils (*e.g., Lepidopleurus davolii* Laghi, 2005), (2) extinct species with names consisting of numbers or letters (e.g. *Lepidopleurus* sp. I Sulc, 1936), (3) indeterminate extinct species placed in valid genera (*e.g., Helminthochiton* sp. Plas, 1972), (4) named extinct species in indeterminate genera (*e.g.*, "Chiton" *cordiformis* Sandberger, 1845), (5) indeterminate taxa (*e.g.*, "unidentified chiton valves," Hoover 1981), (6) extant species with a fossil record

Table 1. Countries with fossil chiton occurrences grouped by geographic regions.

Geographic region	Countries
Africa	Algeria, Eritrea, Ethiopia, Morocco, South Africa, Tanzania
Asia	China, India, Japan, Malaysia, Russia, Thailand
Australasia	Australia, Borneo, Fiji, Indonesia, Marshall Islands, New Zealand, Palau
Europe	Austria, Belgium, Bulgaria, Czech Republic, Denmark, France, Germany, Greece, Hungary, Ireland, Italy, The Netherlands, Norway, Poland, Portugal, Romania, Slovakia, Spain, Svalbard, Sweden, Ukraine, United Kingdom
North America	Bahamas, Canada, Cayman Islands, Jamaica, Mexico, Puerto Rico, United States
South America	Argentina, Brazil, Chile, Columbia, Uruguay, Venezuela

(*e.g.*, *Mopalia muscosa* (Gould, 1846)), and (7) geographic occurrences reported from localities other than type localities. The first reports of extant species were considered equivalent to type localities of extinct species. Affinities (cf., aff.), variations, and subspecies were treated as geographic occurrences and placed in group seven rather than as taxonomic occurrences in one of the other groups.

Data analysis

The collector curve approach (Weller 1952, Paul 2003, Fountaine *et al.* 2005, Tarver *et al.* 2007) was used to investigate the sampling completeness of the chiton fossil record. Assuming no decrease in effort, collector curves are exponential as discovery rates increase and become asymptotic and sigmoid when virtually every fossil taxon that has been preserved has been found (Benton 1998, Fountaine *et al.* 2005, Tarver *et al.* 2007). Collector curves, thus, are plots of the cumulative number of discoveries against some measure of collecting effort. The number of new taxa described per year and the number of fossil occurrences reported each year were used as the measure of total collecting effort. Neither approach assumes that the workers are constant. The first approach shows the rate at which workers are finding new taxa. The second approach accounts for workers finding few new taxa. In the latter case, publication history tends to move away from descriptions and into broader topics such as preservation potential and biogeography (Tarver *et al.* 2007). Publication history, thus, was assessed by categorizing the authors' primary reasons for reporting

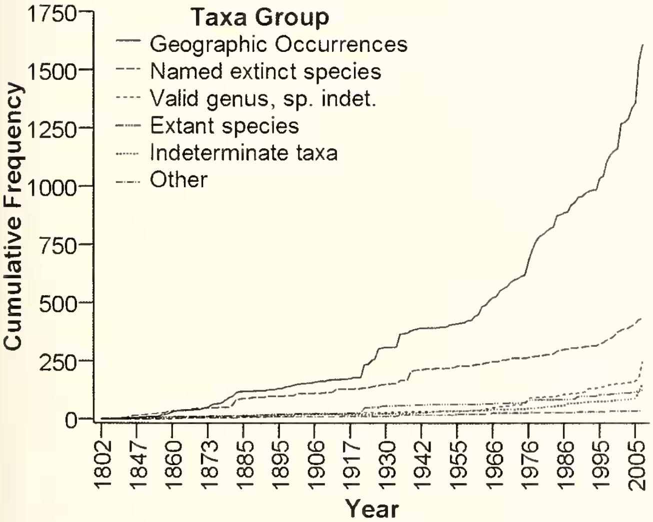

Figure 1. Collector curves for the seven groups of valid chiton taxa. The fossil record represented by the database is comprised mostly of geographic occurrences of previously described taxa discovered at localities other than type localities. The group of species with names consisting of numbers or letters and named species of indeterminate genera have been collapsed into one group labeled 'other' for clarity because these groups each represent less than 1% of the data.

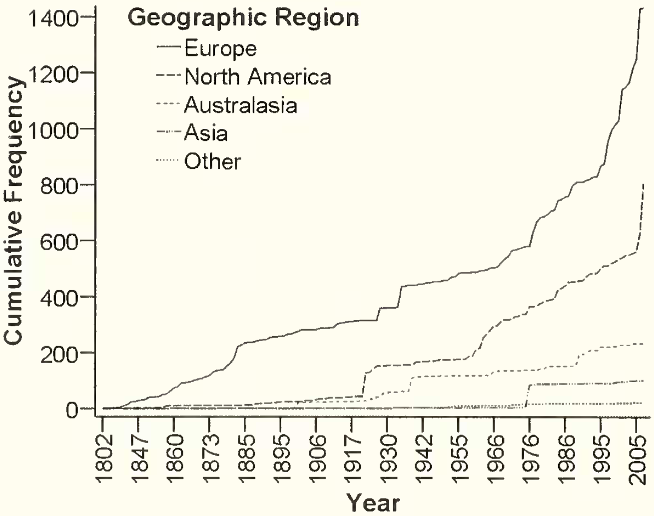

Figure 2. Collector curves for all fossil chiton occurrences reported by geographic region (see Table 1 for listing of the countries in each region). Countries in Africa and South America have been combined into one group labeled "other" for clarity because these two regions represent less than 1% of the data.

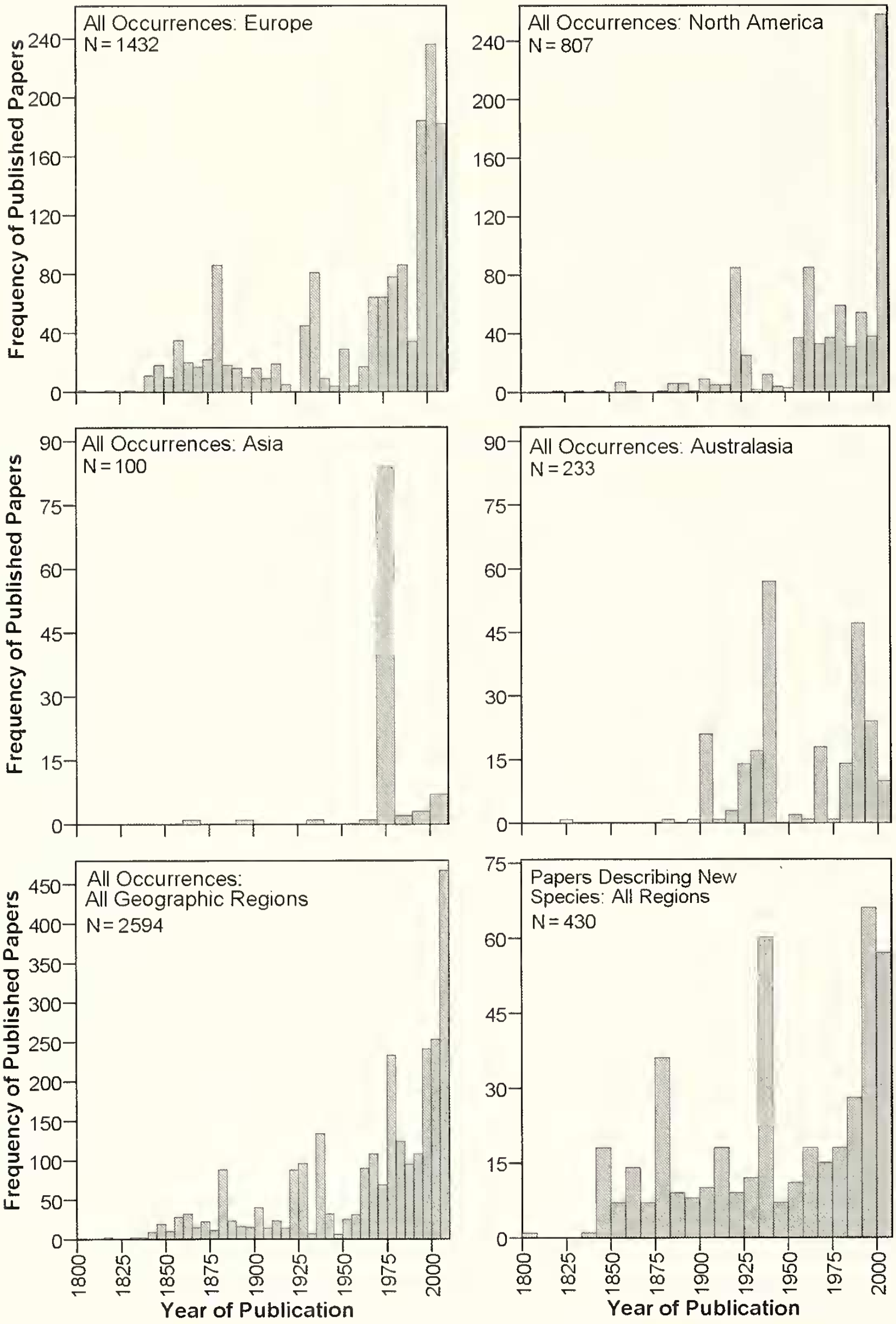

Figure 3. Histograms comparing the frequency of published papers reporting occurrences of all seven groups of fossil chiton taxa from Europe, Australasia, North America, and all geographic regions as a measure of worker effort. African and South American regions with less than 100 publications total are not shown. The publication frequency of new taxa described from all geographic regions also is shown. Note: y-axis scale varies among histograms.

the fossils based on the subject area that constituted the bulk of each publication. For example, the taxonomic group consisted of papers with systematic paleontology sections comprising most of the article. The other categories consisted of general faunal papers that did not fit into another group, biostratigraphic papers, taphonomic papers, or paleoecologic papers.

RESULTS AND DISCUSSION

At the time of analysis, the database comprised 2594 occurrences of 900 chiton taxa. Of the 900 taxa, 430 are valid fossil species named and described from 1802 through 2007, 123 are extant species with a fossil record, and 247 are indeterminate species. The 900 taxa are placed in 95 genera, 31 families, 9 suborders, and 4 orders of the Class Polyplacophora. In comparison, Van Belle (1981) listed 250 named and 49 indeterminate fossil species and a few extant species with a fossil record. Smith's (1960) compilation included 293 named and unnamed species known only as fossils and 59 extant species with a fossil record. Smith and Hoare (1987) reported 153 Paleozoic named species and 23 indeterminate taxa. Schwabe (2005) reported 368 named species known only as fossils. Despite the importance of these previous fossil catalogues, named fossil and extant species combined represent only about 21.3% of all 2594 fossil occurrences in the current database. Most of the data (61.0%) consists of previously identified species that occurred at localities other than type localities. The large numbers of geographic occurrences suggest that the fossil record is richer than previously indicated in the literature.

The fully exponential pattern of the collector curves indicates that sampling of fossil chitons has been inadequate for all taxonomic groups (Fig. 1) and geographic regions (Fig. 2). The stepped Asian curve and roughly asymptotic Australasian curves potentially suggest that the sampling records are complete for these regions. The combined African-South American collector curve also appears relatively flat, but this is partly due to limited data and partly due to the scale of the graph required to show the Australasian, European, and

North American curves that represent the majority of data. However, flattening of collector curves also may be caused by decreased collecting effort (Tarver *et al.* 2007). As a measure of collecting effort, decreased frequency in the number of published papers suggests that flattening of the Asian and Australasian collector curves are due to decreased efforts rather than failure to find new species (Fig. 3). In comparison, the increased frequency of papers on European occurrences suggests collecting efforts have risen in the last few decades. The corresponding European collector curve has not reached an asymptote (Fig. 2), indicating continued high rates of discovery of new taxa. In North America, collecting efforts have remained relatively high from 1960 to the present but the collector curve still is in the exponential phase, similarly indicating high discovery rates of new taxa. The incomplete sampling records thus result from heterogeneity in collecting effort focused on fossil chitons.

The frequency of papers describing new species from all seven geographic regions shows a fairly steady increase from 1950 to the present (Fig. 3). However, the data also suggest there is much information in the fossil record of chitons that has yet to be tapped. Most papers were published for the purposes of describing new taxa (Fig. 4). Taxonomic reports comprise most of the reported occurrences (N = 2238, 86.2%), although some occurrences were reported as part of general fauna (N = 205, 7.9%) or biostratigraphic studies (N = 95, 3.7%). Few fossil chitons were reported as part of taphonomic (N = 5, 0.2%) or ecologic (N = 51, 2.0%) studies. The implication is that the range of research on fossil chitons still is mostly in the discovery phase and has yet to broaden.

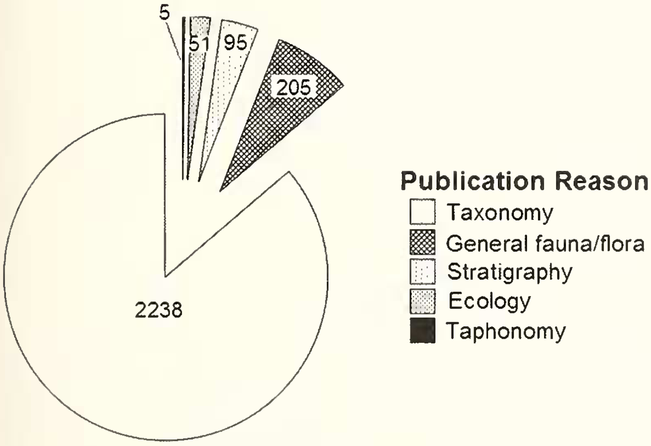

Figure 4. Pie chart showing the distribution of the reasons for publication of papers reporting occurrences of fossil chitons. Reasons were determined by the subject areas that constituted the bulk of each publication: taxonomy, systematic descriptions; biostratigraphy, temporal correlations; paleoecology, paleoecological analyses; taphonomy, taphonomic analyses; general fauna/flora, papers not fitting into previous categories. Numbers shown in each slice indicate the number of publications in each category.

Although the collector curves indicate inadequate sampling of all seven groups of fossil chiton taxa through the Phanerozoic (Fig. 5), the data may be sufficient for some geobiological studies depending on the geologic time and/or geographic region being investigated. Some geologic time periods and geographic fossil records of chitons are more complete than others due to the heterogeneity in collecting effort. For example, most fossil species occur in the Carboniferous and Cenozoic (Eocene and Miocene to Pleistocene, Fig. 6). Although the shapes of the Cenozoic and Paleozoic curves are similar among groups of taxa, active research and focused collecting efforts can be attributed to a limited number of researchers that have contributed to the increases in both cases. Richard Hoare, as author or coauthor, has described thirty-one new Carboniferous chiton species, resulting in a more complete record for the period. The Cenozoic increase may be attributed to the more complete sampling of Holocene biota referred to as the 'pull of the Recent' (Raup 1979, Foote 2000, Alroy *et al.* 2001, Peters and Foote 2001). However, Bruno Dell'Angelo, as author or coauthor, accounts for 242 or 11.8% of the Cenozoic occurrences, most in the Mediterranean, suggesting that focused collecting effort has resulted in a more complete Cenozoic record for the European region. In comparison, the Mesozoic collector curves suggest severely inadequate sampling of chitons for that period.

Temporal gaps shown by this analysis do not necessarily equate to non-existence of chitons in past ecosystems. Although the non-logistic nature of the collector curves indicates that at least some gaps in the current dataset are due to sampling bias, the generally poor preservation states of most fossils indicate that taphonomic biases also may have been a contributing factor. Paleoecologic data show that Paleozoic chitons mostly inhabited shallow coastal environments similar to the settings inhabited by most modern chiton species (Dunlop 1915, 1922, Frederickson 1962, Smith and Toomey 1964, Kues 1978, Yancey and Stevens 1981, Gerk and Levorson 1982, Hoare and Smith 1984, Debrock *et al.* 1984, Farrell 1992, Vendrasco 1999, Cherns 1999, Hanger *et al.* 2000, Hoare 2001, Cherns 2004, Vendrasco and Runnegar 2004). There is no reason to assume that the preservation potential of chitons in the past differed greatly from that in modern environments. Most modern chitons tend to live in intertidal or shallow subtidal erosional environments that are rarely preserved even where fossil deposits are extensive (*e.g.*, California Miocene). Modern chitons are more rarely found living in relatively deep water or on muddy bottoms, but species diversity in such cases is much lower relative to shallow water communities. Fossil chitons interpreted to have lived on muddy bottoms or in deeper water are rare, but have been reported (Hoare *et al.* 1972, Lang and Chlupac

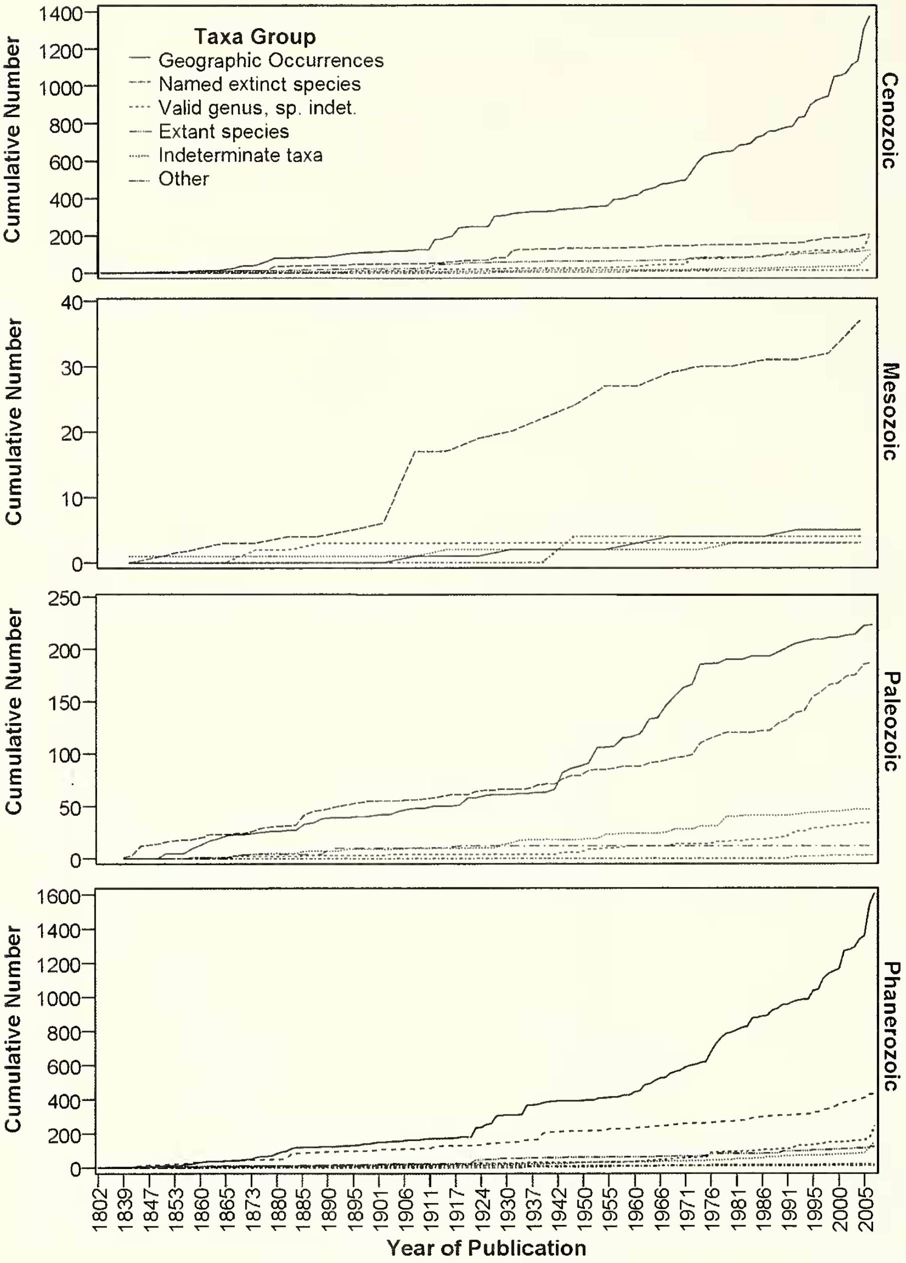

Figure 5. Collector curves for each taxa group of fossil chiton occurrences reported by geologic era and for Phanerozoic. Not all seven groups have been reported from all three eras.

1975, Richardson 1980, Dell'Angelo and Palazzi 1994, Palazzi and Villari 1994, Goedert and Campbell 1995, Squires and Goedert 1995, Remia and Taviani 2005, Kiel and Goedert 2006). As with modern settings, diversity appears to be lower relative to the shallow water assemblages.

Observed changes in chiton diversity through time (Fig. 6) do not correlate to degrees of preservation or skeletal completeness. In general, changes in species numbers through geologic time indicate chitons were affected by mass extinctions (Fig. 6). For example, decreased numbers of species in the Paleocene imply that chitons were affected by the end-Cretaceous mass extinction. The species numbers increased in the Eocene following an apparent slow recovery through the Paleocene. The mean number of species per occurrence (≈ locality) used as a proxy for diversity suggests that chiton diversity has remained relatively constant through the Phanerozoic (Fig. 6). Pleistocene diversity is not significantly greater than Eocene or Late Permian diversity, for example. Whether these patterns are artifacts of the sampling inadequacy or real trends remain to be investigated. Continued active collection and study of fossil chitons should be encouraged because the non-logistic nature of the collector curves suggest that many more fossil chiton species remain to be found and described. Recent discoveries have been instrumental in demonstrating that Paleozoic chitons were more diverse in form than modern chitons (*e.g.*, Pojeta *et al.* 2003, Vendrasco *et al.* 2004). Further analysis will investigate large-scale evolutionary and ecological patterns in the data with the goal of assessing the fidelity of the chiton fossil record after correcting for the sampling bias indicated in this preliminary analysis.

ACKNOWLEDGMENTS

Financial assistance to S.P. was provided by grants from the Department of Geological Sciences and Women in Science Fellowship through Indiana University. D.E. acknowledges a sabbatical fellowship supported by the National Evolutionary Synthesis Center (NESCent), NSF #EF-0423641. Richard Van Belle's (1981) *Catalogue of Fossil Chitons* provided D.E. with the initial inspiration for a computerized version of a fossil chiton species database and, likewise, Theo Engesser provided D.E. with an independent, unpublished compilation of nominal fossil species. Bruno

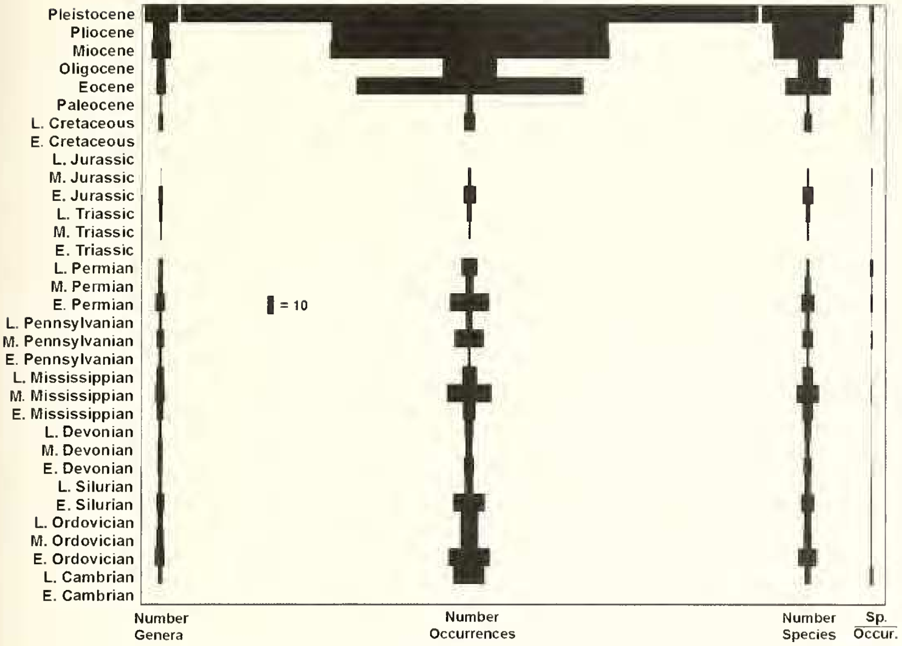

Figure 6. Diagram showing numbers of genera, occurrences, and species by epoch. Sp./ occur., number of species per occurrence. Bar width of $N = 10$ shown for scale.

Dell'Angelo contributed an extensive list of references on chitons. R. Hendrickson provided critical proof reading. Comments by J. Pojeta and an anonymous reviewer greatly improved the original manuscript.

LITERATURE CITED

Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. M. A. I. Low, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. Sepkoski, Jr., M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Science* **98**: 6261-6266.

Baluk, W. 1984. Additional data on chitons and cuttlefish from the Korytnica Clays (middle Miocene: Holy Cross Mountains, central Poland). *Acta Geologica Polonica* **34**: 281-297.

Bellomo, E. and B. Sabelli. 1995. A new addition to the Mediterranean Pleistocene boreal guests: *Hanleya nagelfar* (Lovén, 1864) (Mollusca, Polyplacophora) from Calabria (S. Italy). *Bollettino della Societa Paleontologica Italiana* **34**: 201-204.

Benton, M. J. 1993. *The Fossil Record 2.* Chapman & Hall, London.

Benton, M. J. 1998. The quality of the fossil record of vertebrates. *In*: S. K. Donovan and C. R. C. Paul, eds., *The Adequacy of the Fossil Record.* Wiley, New York. Pp. 269-303.

Benton, M. J., M. A. Wills, and R. Hitchin. 2000. Quality of the fossil record through time. *Nature* **403**: 534-537.

Bischoff, G. C. 1981. *Cobrephora* n. g., representative of a new polyplacophoran order Phosphatoloricata with calcium phosphatic shells. *Senckenbergiana Lethaea* **61**: 173-215.

Cherns, L. 1999. Silurian chitons as indicators of rocky shores and lowstand on Gotland, Sweden. *PALAIOS* **14**: 172-179.

Cherns, L. 2004. Early Palaeozoic diversification of chitons (Polyplacophora, Mollusca) based on new data from the Silurian of Gotland, Sweden. *Lethaia* **37**: 445-456.

Cleveringa, P., T. Meijer, R. J. van Leeuwen, H. de Wolf, R. Pouwer, T. Lissenberg, and A. W. Burger. 2000. The Eemian stratotype locality at Amersfoort in the central Netherlands: A reevaluation of old and new data. *Geologie en Mijnbouw* **79**: 197-216.

Dell'Angelo, B. and S. Palazzi. 1994. Prima segnalazione di *Connexochiton platynomenus* Kaas, 1979 nel Pleistocene calabro. [First report of Connexochiton platynomenus Kaas, 1979 in the Pleistocene of Calabria]. *Bollettino Malacologico* **29**: 233-236 [In Italian].

Debrock, M. D., R. D. Hoare, and R. H. Mapes. 1984. Pennsylvanian (Desmoinesian) Polyplacophora (Mollusca) from Texas. *Journal of Paleontology* **58**: 1117-1135.

Dunlop, R. 1915. Notes on the discovery of fossil chitons in Fife. *Transactions of the Geological Society of Glasgow* **15**: 167-173.

Dunlop, R. 1922. Notes on the chitons of Woodmill. *Transactions of the Geological Society of Glasgow* **17**: 75-76.

Eernisse, D. J. 2001. A compilation of chiton fossil species. *PaleoBios* **21**: 2.

Farrell, J. R. 1992. The Garra Formation (Early Devonian: Late Lochkovian) between Cumnock and Larras Lee, New South Wales, Australia: Stratigraphic and structural setting, faunas, and community sequence. *Palaeontographica Abteilung* (A) **222**: 1-41.

Foote, M. 2000. Origination and extinction components of taxonomic diversity: General problems. *Paleobiology* **26**: 74-102.

Fountaine, T. M. R., M. J. Benton, G. J. Dyke, and R. L. Nudds. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society of London* (B) **272**: 289-294.

Frederickson, E. A. 1962. *Helminthochiton* from the Pennsylvanian of Oklahoma. *Oklahoma Geology Notes* **22**: 298-302.

Gerk, A. J. and C. O. Levorson. 1982. Unusual beach deposits in oolite carbonate environments: Mississippian and Recent. *Proceedings of the Iowa Academy of Science* **89**: 68-70.

Goedert, J. L. and K. Campbell. 1995. An early oligocene chemosynthetic community from the Makah formation, Northwestern Olympic Peninsula, Washington. *The Veliger* **38**: 22-29.

Hanger, R. A., R. D. Hoare, and E. E. Strong. 2000. Permian Polyplacophora, Rostroconchia, and problematica from Oregon. *Journal of Paleontology* **74**: 192-198.

Hoare, R. D. 2001. Early Mississippian Polyplacophora (Mollusca) from Iowa. *Journal of Paleontology* **75**: 66-74.

Hoare, R. D., M. T. Sturgeon, and T. B. Hoare. 1972. Middle Pennsylvanian (Allegheny Group) Polyplacophora from Ohio. *Journal of Paleontology* **46**: 675-680.

Hoare, R. D. and A. G. Smith. 1984. Polyplacophora (Mollusca) from West Texas. *Journal of Paleontology* **58**: 82-103.

Hoare, R. D. and R. H. Mapes. 2000. New data on the genus *Diadeloplax* Hoare and Mapes, 1995. *Journal of Paleontology* **74**: 976-978.

Hoare, R. D. and J. Pojeta, Jr. 2006. Ordovician Polyplacophora Mollusca from North America. *Journal of Paleontology* **80**: 1-27.

Hoover, P. 1981. Paleontology, taphonomy and paleoecology of Palmarito Formation (Permian of Venezuela). *Bulletins of American Paleontology* **80**: 1-313.

Itoigawa, J., M. Kuroda, A. Naruse, and H. Nishimoto. 1976. Polyplacophora assemblages from the Pleistocene formations of Boso and Miura peninsulas, environs of Tokyo, Japan. *Mizunami shi Kadeki Hakubutsukan Kenkyu Hokoku* **3**: 171-204 [In Japanese].

Kaas, P. and R. A. Van Belle. 1985. *Monograph of Living Chitons (Mollusca: Polyplacophora): Order Neoloricata—Lepidopleurina Volume 1*. E. J. Brill Publishers, Leiden, The Netherlands.

Kiel, S. and J. L. Goedert. 2006. A wood-fall association from Late Eocene deep-water sediments of Washington State, USA. *PALAIOS* **21**: 548-556.

Kirkby, J. W. 1859. On the Permian Chitonidae. *Quarterly Journal of the Geological Society of London* **15**: 607-626.

Kues, B. S. 1978. Polyplacophora from the Salem Limestone (Mississippian) in central Indiana. *Journal of Paleontology* **52**: 300-310.

Laghi, G. F. 1984. Sorprendente densita di *Chiton saeniensis* n sp in sabbie gialle plioceniche dei dintorni di Serre di Rapolano Siena. [An astonishing density of *Chiton saeniensis* n. sp. in the Pliocene yellow sands of the Serre di Rapolano region, Sienna] *Bollettino Museo Regionale di Scienze Naturali* **2**: 555-564 [In Italian].

Lang, V. and I. Chlupac. 1975. New finds of trilobites in the Culm of the Drahanska vrchovina Upland (Moravia, Czechoslovakia). *Vestnik Ústredniho ústavu geologického* **50**: 377-344.

Lindberg, D. R. 1985. Aplacophorans, monoplacophorans, polyplacophorans, scaphopods; the lesser classes. *In*: T. W. Broadhead, ed., *Mollusks: Notes for a Short Course*. University of Tennessee, Knoxville. Pp. 230-247.

Palazzi, S. and A. Villari. 1994. Malacofaune batiali plio-pleistoceniche del Messinese 1: Venetico Marina. [Plio-Pleistocene bathyal malacofauna of Messinese 1: Marine Venetico] *Il Naturalista Siciliano* **18**: 73-106 [In Italian].

Paul, C. R. C. 2003. Ghost ranges. *In*: P. C. J. Donoghue and M. P. Smith, eds., *Telling the Evolutionary Time: Molecular Clocks and the Fossil Record*. CRC Press, London. Pp. 91-106.

Peters, S. E. and M. Foote. 2001. Biodiversity in the Phanerozoic: A reinterpretation. *Paleobiology* **27**: 583-601.

Pojeta, J. J., D. J. Eernisse, R. D. Hoare, and M. D. Henderson. 2003. *Echinochiton dufoei*: A new spiny Ordovician chiton. *Journal of Paleontology* **77**: 646-654.

Qian, Y. and S. Bengston. 1989. Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* **24**: 1-156.

Raup, D. M. 1976a. Species diversity in the Phanerozoic: A tabulation. *Paleobiology* **2**: 279-288.

Raup, D. M. 1976b. Species diversity in the Phanerozoic: An interpretation. *Paleobiology* **2**: 289-297.

Raup, D. M. 1979. Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* **13**: 85-91.

Remia, A. and M. Taviani. 2005. Shallow-buried Pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. *Facies* **50**: 419-425.

Puchalski, S. S. 2005. *Taphonomy of Chitons (Mollusca, Polyplacophora) and the Chiton Fossil Record*. M.S. Dissertation, Indiana University, Bloomington, Indiana.

Richardson, E. S. J. 1980. Life at Mazon Creek. *In*: R. L. J. Langenheim and C. J. Mann, eds., *Middle and Late Pennsylvanian Strata on Margin of Illinois Basin, Vermilion County, Illinois, Vermillion and Parke Counties, Indiana*. Annual Field Conference, Society of Economic Paleontologists and Mineralogists, Great Lakes Section. Pp. 217-224.

Schwabe, E. 2005. A catalogue of Recent and fossil chitons (Mollusca: Polyplacophora) Addenda. *Novapex* **6**: 89-105.

Sepkoski, J. J. J. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology* **363**: 1-560.

Sigwart, J., S. B. Andersen, and K. I. Schnetler. 2007. First record of a fossil chiton from Denmark Polyplacophora: Leptochitonidae and its phylogenetic affinities. *Journal of Systematic Palaeontology* **5**: 123-132.

Sirenko, B. 2006. New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus: The Japanese Journal of Malacology* **65**: 27-49.

Squires, R. L. and J. L. Goedert. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. *The Veliger* **38**: 47-53.

Smith, A. B. 2001. Large-scale heterogeneity of the fossil record: Implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London* (B) **356**: 351-367.

Smith, A. G. 1960. Amphineura. *In*: J. B. Knight, L. R. Cox, A. M. Keen, A. G. Smith, R. L. Batten, E. L. Yochelson, N. H. Ludbrook, R. Robertson, C. M. Yonge, and R. C. Moore, eds., *Treatise on Invertebrate Paleontology Part I, Mollusca 1*. Geological Society of America and University of Kansas, New York. Pp. 41-76.

Smith, A. G. 1973. Fossil chitons from the Mesozoic—a checklist and bibliography. *Occasional Papers of the California Academy of Sciences* **103**: 1-30.

Smith, A. G. and D. F. Toomey. 1964. Chitons from the Kindblade Formation (Lower Ordovician), Arbuckle Mountains, southern Oklahoma. *Oklahoma Geological Survey Circular* **66**: 1-41.

Smith, A. G. and R. D. Hoare. 1987. Paleozoic Polyplacophora: A checklist and bibliography. *Occasional Papers of the California Academy of Sciences* **146**: 1-71.

Tarver, J. E., S. J. Brady, and M. J. Benton. 2007. The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Paleontology* **50**: 177-184.

Van Belle, R. A. 1981. *Catalogue of Fossil Chitons (Mollusca: Polyplacophora)*. W. Backhuys, Rotterdam, The Netherlands.

Vendrasco, M. J. 1999. *Early evolution of the Polyplacophora (chitons)*. Ph.D. Dissertation, University of California, Los Angeles, California.

Vendrasco, M. J. and B. N. Runnegar. 2004. Late Cambrian and Early Ordovician stem group chitons (Mollusca: Polyplacophora) from Utah and Missouri. *Journal of Paleontology* **78**: 675-689.

Vendrasco, M. J., T. E. Wood, and B. N. Runnegar. 2004. Articulated Palaeozoic fossil with 17 plates greatly expands disparity of early chitons. *Nature* **429**: 288-291.

Weller, J. M. 1952. Analysis of trilobite generic nomenclature and its implications regarding paleontology. *Journal of Paleontology* **26**: 137-147.

Westrop, S. R. and J. M. Adrain. 2001. Sampling at the species level: Impact of spatial biases on diversity gradients. *Geology* **29**: 903-906.

Yancey, T. E. and C. H. Stevens. 1981. Early Permian Fossil Communities in Northeastern Nevada and Northwestern Utah. *In*: J. Gray, A. J. Boucot, and W. B. N. Berry, eds., *Communities of the Past*. Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania. Pp. 243-268.

Yü, W. 1987. Yangtze micromolluscan fauna in Yangtze region of China with notes on Precambrian-Cambrian boundary. *In*: *Stratigraphy and Palaeontology of Systemic Boundaries in China: Precambrian-Cambrian Boundary*. Nanjing Institute of Geology and Palaeontology, Nanjing University Publishing House, Nanjing. Pp. 19-275.

Yü, W. 2001. The earliest Cambrian Polyplacophorans from China. *Records of the Western Australian Museum* **20**: 167-185.

Submitted: 10 April 2007; **accepted:** 26 November 2007; **final revisions received:** 1 February 2008